THE GENETICS OF THE GOLDEN-WINGED × BLUE-WINGED WARBLER COMPLEX

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PERHAPS the best known and most thoroughly documented case of hybridization between species of wild birds, at least in the North American avifauna, is that of the Golden-winged Warbler (*Vermivora chrysoptera*) and Blue-winged Warbler (*V. pinus*). These two species seem to hybridize more or less freely wherever their ranges overlap, producing two general hybrid types which were originally named as species: the Brewster's Warbler ("*Vermivora leucobronchialis*") and the Lawrence's Warbler ("*V. lawrencei*"). Before the hybrid nature of these two types was thoroughly established, many theories were proposed to account for the interrelationships observed. Some of these theories seem fantastic to the modern student. Early field observations and the various theories were summarized and synthesized by Faxon in two excellent monographs (1911, 1913).

The purpose of this paper is to review briefly what is known of these hybrids, to discuss a commonly accepted genetic explanation for the observed inheritance of characters, and to point out what shortcomings remain in our knowledge of their interrelationships. Original observations on the possible phenotypical detection of heterozygotes will also be presented.

The Parental Species

The Blue-winged and Golden-winged Warblers are neither strictly sympatric nor strictly allopatric. In general, the Blue-winged has the more southern breeding range, but there is a broad strip, roughly through southern New England, southern New York, New Jersey, Pennsylvania, Ohio, southern Michigan, northern Illinois and southern Minnesota, where the ranges of the two species overlap. It is in these areas, as would be expected, that the hybrids

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[1] The hybrid warblers shown in the color plate opposite are, from top to bottom:

F_1 Brewster's Warbler. Genotype WwSsPp. American Museum of Natural History specimen No. 380136. New Haven, Connecticut, May 17, 1892.

Back-cross Brewster's Warbler. Genotype WWSSPp. American Museum of Natural History specimen No. 392172. Bonilla, Costa Rica, September 27, 1920.

Lawrence's Warbler. Genotype wwsspp. American Museum of Natural History, L. C. Sanford collection No. 10846. Stratfield, Connecticut, May 19, 1917.

Heterozygous Golden-winged Warbler. Genotype WwSsPP. Chicago Natural History Museum No. 148778. New Haven, Connecticut, May 11, 1900.

Crossover-type Golden-winged Warbler. Genotype WWSspp. American Museum of Natural History No. 506277. Cumbre de Valencia, Venezuela, January 31, 1910.

Crossover-type Blue-winged Warbler. Genotype wwSsPP. American Museum of Natural History No. 380055. New Haven, Connecticut, May 17, 1893.

are found most commonly. In a number of outlying areas, either the Blue-winged or the Golden-winged is found only as an intruder, often recent, into the range of the other species. In such areas, the hybrids are quite sporadic (see Parkes, 1949, for a summary of such a situation in central and western New York). On the other hand, in certain areas where the parents are almost equally common, the hybrids are frequently observed. This is especially true of the area around southern New York, Connecticut and northern New Jersey. Most of the hybrid specimens I have examined are from this general area.

There is a small amount of ecological distinction between these two species in the areas where their ranges overlap, but the ecological preferences seem to overlap just as do the ranges. In general, the Golden-winged Warbler prefers the higher and more wooded portions of slopes, the Blue-winged the lower and more open. There is much local variation, occasionally even a reversal of the usual situation. Both species commonly live "in clearings, at the edge of the forest, and in abandoned fields, and it is probable that the hybridization is of recent date and caused by man-made habitat disturbances" (Mayr, 1942: 262). The theory of recent origin of the hybridization, whether or not assisted by man, is given added support by the fact that, although the region where the hybrids are now most frequent was one of the earliest to be studied, faunally, in the United States, the Lawrence's and Brewster's Warblers were not described until 1874. A few earlier specimens have since turned up in old collections.

The suggestion that *Vermivora chrysoptera* and *V. pinus* be considered conspecific has received little modern support, even among the most ardent of "lumping" taxonomists. The two parental types are too distinct to warrant such a step, and Mayr (*loc. cit.*) has called our attention to the fact that "hybridization has not led to a blurring of the border between the two species."

The Blue-winged and Golden-winged Warblers differ in three readily perceptible major color characters. These are (1) the ground color of the body (especially as regards the white or yellow of the underparts), (2) the presence or absence of a black throat-patch, and (3) the number and color of the wing-bars. Genetic speculation seems hitherto to have been limited to the first two of these; all three will be discussed in this paper.

Mating Behavior of Hybrids

It has long been known that the hybrids were fertile, and the literature abounds with breeding records for both the Brewster's and Lawrence's Warblers. There is an unusual phenomenon connected with the breeding of these hybrid types. In surveying published breeding records, one inevitably reaches the conclusion that the hybrids do not breed *inter se*, but only back-cross with birds that are at least phenotypically (that is, of the external appearance) of one of the parental types. Several authors have remarked upon the absence of records

of hybrid-hybrid matings (Faxon, 1911: 71–73). I have been able to locate but two published references to matings in which both of the parents are stated to have been hybrids. Sutton (1928: 206) recorded a nest found on June 6, 1922, near Hartstown, Pennsylvania, containing three heavily incubated eggs and two young birds. The supposed parent birds were taken, and were mailed to Sutton in the flesh by the collector, John G. Thomas. Both were of the Brewster's Warbler type. The male had an immaculately white breast, while the underparts of the female were strongly washed with yellow. Unfortunately these specimens were not preserved.

Hicks (1929: 44) recorded "a pair of typical Brewster's Warblers feeding young" in Hocking County, Ohio, on June 11–12, 1927. In his later list of Ohio birds (1935: 168), he modified this statement to read "Two Brewster's Warblers, *apparently* mated and feeding young . . ." (italics mine). Further data on this brood would undoubtedly have been gathered by Hicks had he realized the unique nature of the observation.

These appear to be the only recorded matings between hybrid warblers. While neither record is conclusive, each tends to weaken the concept that hybrids mate in back-crosses *only*. On the basis of presently available data, there certainly seems to be a marked *tendency* toward back-crosses. It must be acknowledged that over much of the range of the hybrids, availability of mates is the primary factor. In a region such as central New York, where the Golden-winged is the dominant species and the Blue-winged of purely fortuitous occurrence, a hybrid would be limited to Golden-winged Warblers in its choice of mates. However, in a well-studied area such as the lower Hudson Valley, where the hybrids are of regular occurrence (it has been said that they may occasionally outnumber the parental species locally), it would seem that hybrid-hybrid matings would have been recorded if no preferential factor or other reproductive barrier were in operation.

The best recent summary of extensive field observations of these warblers is that of Carter (1944). His studies would seem to indicate the presence of some preferential factor in mating, at least in this particular study area. A banded individual male Brewster's Warbler was observed for six successive years, and his mate and nest found in five of these years. Each year he mated with a female Golden-winged Warbler. Carter and his co-workers were of the opinion, based on banding and individual variation, that the female was a different individual each year. That female warblers other than Golden-winged were available as mates is indicated by the fact that in this small (about four acres) area in Passaic County, New Jersey, during this six-year study, observations were made of the following: a male Lawrence's x female Golden-winged nesting, a male Blue-winged x female Golden-winged nesting, four additional Brewster's Warblers, and two additional Lawrence's Warblers. Young birds were raised successfully in all of the nestings observed, and certain birds

banded as nestlings returned to the same area in subsequent years. Phenotypically, some of these young birds were certainly hybrids. Therefore there would seem to have been in the neighborhood an ample supply of hybrid birds from which the male Brewster's Warbler might have selected a mate. He did not do so, however, nor were any of the other hybrids in the study area known to have taken hybrid mates.

Although Carter's observations are, to my knowledge, the only published records showing the mating behavior of an individual hybrid *Vermivora* over a number of years, there are a number of instances from within single breeding seasons which support the thesis that hybrids do not mate with hybrids even when such mates are available. Faxon, for instance, described (1913: 311) the situation in 1910 in a swamp near Lexington, Massachusetts. The *Vermivora* population here consisted of a mated pair of Golden-winged Warblers; two female Brewster's Warblers, each mated to a male Golden-winged; and a male Brewster's Warbler which remained unmated throughout the season. (It is, of course, impossible to say *why* the male Brewster's Warbler was not paired with one of the female hybrids.) Since there were four male warblers and only three females in the area, one of the males must obviously have been forced to remain unmated. Possibly chance dictated that the unmated male should be the Brewster's; however, observations of situations of this sort are frequent enough to warrant the discounting of chance as the only factor involved.

It has been suggested that hybrid males may remain unmated because of a low adaptability in competing for mates. Male Brewster's Warblers are, however, frequently found mated to female Golden-winged Warblers in Golden-winged country where plenty of male Golden-winged competition exists.

Genetics of the Throat-patch

One of the major color differences between the Blue-winged and Golden-winged Warblers is the black throat-patch of the latter. Correlated with the presence of this patch is the broadening of the black transocular line of *pinus* into a black mask extending to the ear coverts in *chrysoptera*. This transocular mask I shall discuss later in this paper. The presence or absence of the throat-patch is believed to result from the action of a single gene.

The first use of letter symbols for the characters involved in these crosses seems to have been that of Nichols (1908). His notation has been employed by Faxon (1911: 73) and more recently by Pough (1946: 153). For the sake of convenience, therefore, Nichols' symbols will be used in the remainder of this paper. According to this notation, the allele for the dominant plain throat of the Blue-winged Warbler is assigned the symbol P. The black-throated condition, therefore, is represented by p. A homozygous ("pure" of many early authors) Blue-winged Warbler would carry the genes PP, and a homozygous Golden-winged Warbler pp. The first generation (F_1) hybrid, receiving a gene from either

parent, would have the heterozygous ("impure") genotype Pp. As P is dominant over p, this hybrid would have a plain throat.

Genetics of Underparts Color

The diagram given by Pough (*loc. cit.*) ascribes the presence or absence of the throat-patch and the white or yellow of the underparts to the action, respectively, of two single genes. In the case of throat-patch inheritance, this seems to be correct. Inheritance of underparts color, however, does not involve simple presence- or absence-characters such as those determining color of the throat-patch, as will be seen later. For purposes of preliminary explanation let us assume a single gene to control underparts color, of which the allele W (white) is dominant over the allele w (yellow). Thus the homozygous Golden-winged Warbler would have the genotype WWpp, since it has white underparts and a black throat-patch. Similarly, the Blue-winged Warbler, having yellow underparts and a plain throat, would have the genotype wwPP. The F_1 hybrid would have the genotype WwPp, the new combination of dominants thus giving us a white-breasted, plain-throated bird. This is obviously the hybrid type known as Brewster's Warbler.

The Origin of Lawrence's Warbler

Pough's diagram illustrates the theoretical Mendelian ratio in the F_2 generation resulting from crossing two F_1 Brewster's Warblers. Phenotypically, the expected ratio in the offspring of such crosses would be 9 Brewster's to 3 Golden-winged to 3 Blue-winged to 1 homozygous recessive (wwpp) bird. This last type would have yellow underparts and a black throat-patch: in other words, be a Lawrence's Warbler.

We have seen earlier that the Brewster's x Brewster's cross illustrated by Pough represents the exception in nature. I therefore undertook to compute the various means by which the double recessive, Lawrence's Warbler, might be recovered by crossing hybrids with birds of one or the other parental phenotype. There are a number of possible crosses by which this might be accomplished. In all cases it must be assumed that one or both parents, although phenotypically of one of the parental types, is actually heterozygous for one of the two characters here considered. The theoretical proportion of Lawrence's Warblers in the offspring of various crosses is shown below.

WwPp (F_1 Brew.) x wwPp (hetero. Blue-wing) WwPp (F_1 Brew.) x Wwpp (hetero. Golden-wing)	12.5% Lawrence's
Wwpp (hetero. Gold.-w.) x Wwpp (same) wwPp (hetero. Blue-w.) x wwPp (same) Wwpp (hetero. Gold.-w.) x wwPp (hetero. Blue-wing)	25% Lawrence's
wwpp (Lawrence) x Wwpp (hetero. Golden-wing) wwpp (Lawrence) x wwPp (hetero. Blue-wing)	50% Lawrence's

The relative frequencies in nature of the Brewster's and Lawrence's Warblers support the hypothesis that the latter hybrid represents the homozygous recessive. In the hybridization zone as a whole, the Lawrence's is much less common, although field observations in a limited area of heavy interbreeding may occasionally seem to reverse this proportion. In many localities, only the Brewster's hybrid has thus far been recorded. In the Buffalo, New York, region, for example, a small isolated population of Blue-winged Warblers and a larger population of Golden-winged Warblers have co-existed for many years. There have been a number of records of Brewster's Warbler from year to year, culminating in several breeding records in the past few years. With the subsequent recombination of characters, the appearance in this area of the double recessive Lawrence's Warbler was to be anticipated. This anticipation was realized in the spring of 1949, when the first Lawrence's Warbler was seen in the region.

What is the "Typical" Brewster's Warbler?

Throughout the ornithological literature one finds references to the "typical" Brewster's Warbler. Inevitably this adjective is applied to those Brewster's Warblers whose underparts are immaculately white, without a trace of yellow (Faxon, 1911: 58; Forbush, 1929: 214; Chapman, 1932: 449; Todd, 1940: 495; Peterson, 1947: 188; etc.). The specific epithet "*leucobronchialis*" may in part be responsible for this concept of a white-breasted bird as the 'typical' Brewster's Warbler. In the manuals mention is usually made of the variation in the color of the underparts, as a large proportion of the individuals, instead of being immaculately white beneath, are quite yellowish. Usually this 'variation' is dismissed by calling such birds "individual variants", "intermediates", or "intergrades" with *Vermivora pinus*, or by employing the obsolete genetical term "blending inheritance." With the possibility in mind of finding a genetic theory to account for these yellowish-breasted individuals, I examined 46 specimens of Brewster's Warbler (as well as specimens of the other pertinent forms of *Vermivora*) in the collections of the Chicago Natural History Museum, the American Museum of Natural History, the University of Michigan Museum of Zoology, and the Fuertes Memorial Collection at Cornell University.

It is my belief that the allele W for white underparts is incompletely dominant over the allele w for yellow. Birds which are heterozygous (Ww) for underparts color, therefore, are *basically* white but actually partially yellow. All F_1 Brewster's Warblers resulting from the mating of homozygous Blue-winged (ww) and Golden-winged (WW) parents are of this heterozygous type, the complete genotype of which is WwPp. This genotype may also be recovered in the offspring of a number of other crosses.

According to this theory, Brewster's Warblers with immaculate white underparts must be homozygous for this character, and thus have the genotype WWPp. One cross by which such a genotype may be obtained is that of an F_1

Brewster's Warbler (WwPp) and a homozygous Golden-winged Warbler (WWpp). As we have seen earlier, this is a frequently observed mating in regions of hybridization. One fourth of the offspring of such a cross would be expected to be of the homozygous white-breasted Brewster's type (WWPp). One fourth would be heterozygous yellowish-breasted Brewster's similar to the F_1 (WwPp). One fourth would be homozygous Golden-winged Warblers like the parent (WWpp), and one fourth would be heterozygous Golden-winged Warblers (Wwpp).

Plotting the expected offspring of all possible crosses, and bearing in mind that the initial interspecific cross would be expected to occur most frequently (in the range of the birds as a whole), we find that the yellowish-breasted individuals should outnumber the white-breasted ones by a substantial margin. This is supported by published field observations, and by museum specimens examined, of which 9 were white-breasted and 37 more or less yellow-breasted.

It follows, therefore, that the typical Brewster's Warbler, if by "typical" we mean the first generation offspring of a Blue-winged and a Golden-winged Warbler, has underparts with a definite yellowish tinge. The white-breasted form represents the offspring of a later cross, usually between an F_1 Brewster's and a Golden-winged Warbler.

The Heterozygous Parental Types

If, as postulated above, the allele W for white underparts is incompletely dominant, we should be able to detect the heterozygous (Wwpp) Golden-winged Warblers, for we would expect their underparts below the throat-patch to have a yellowish tinge. In a given museum series of Golden-winged Warblers, only a small number of such individuals would be expected, for two reasons: (1) most specimens usually come from within that part of the range of the species where no opportunity for hybridization exists, and (2) such heterozygotes cannot appear until the second or later hybrid generations. However, at least seven specimens examined fall readily into this category (reference specimens: ♂ CNHM 148778, 148785. ♀ CNHM 148779, AMNH 55041). Carter (1944) mentioned field observations of several individuals of this type in his study area of heavy hybridization. It should be mentioned here that in the normal first winter plumage of *Vermivora chrysoptera* the white underparts are often washed with yellow. However, as will be shown later, these birds can usually be separated from the heterozygotes by the condition of the wing-bars. Spring specimens showing yellow on the underparts are almost certainly heterozygotes.

The genotype of a heterozygous Blue-winged Warbler would be wwPp. Since the allele P for plain throat is believed to be completely dominant over p, it follows that the heterozygous Blue-wings would be externally indistinguishable from the homozygotes. I have never examined nor heard of a specimen of

Brewster's Warbler or Blue-winged Warbler with a faint or partial throat-patch, as might possibly be expected in those individuals heterozygous for the throat-patch character. Specimens of Golden-winged and Lawrence's Warblers in which the throat-patch does not extend as far as the chin represent, not heterozygotes for the throat-patch character, but (according to Dwight, 1900:247) first-year birds. Faxon's field observations of young birds (1911: 66) confirm this point.

The Wing-bars

There is a correlation, hitherto apparently unrecorded, between the color of the underparts and the color of the wing-bars, a correlation which leads me to believe that these two characters are probably rather closely linked in a genetical sense: that the genes determining them are on the same chromosome. The pure white condition of the underparts seems to be linked with the single, broad, pure yellow wing-bar of the Golden-winged Warbler. Yellow underparts, similarly, are linked with the two white wing-bars of the Blue-winged Warbler. Brewster's Warblers with yellowish on the underparts show a definite tendency toward the latter type of wing-bars. Apparently the gene for wing-bars is not only linked with that for underparts color, but exhibits the same sort of behavior in inheritance in that one allele is incompletely dominant over the other. I shall designate the dominant allele for single yellow wing-bar as S; the allele for double white wing-bar is therefore s. Just as the underparts color allele W is incompletely dominant over w, so S is incompletely dominant over s. The F_1 Brewster's Warbler, with the heterozygous wing-bar genotype Ss, has wing-bars intermediate between those of the parent species. This intermediacy is usually manifested by doubleness and whiteness of wing-bar, but the distinctly yellow tips and edges of the white areas of the feathers involved create the gross appearance of two pale yellow wing-bars. Since I have postulated that underparts color and wing-bar color are linked, a bird which is heterozygous for one of these characters would also be heterozygous for the other. It would be expected, therefore, that the heterozygous Golden-winged Warblers described earlier would have intermediate wing-bars, and such is indeed the case.

The wing-bars of the Blue-winged Warbler, being linked with the recessive yellow underparts, should theoretically be consistent. Occasionally, however, a specimen of this species is found to have yellowish wing-bars (reference specimen AMNH 95449). There is a simple genetic explanation for this. Such a bird may have had as one parent a Brewster's Warbler in whose underparts and wing-bar chromosome a crossover had taken place. If the other parent had been a normal Blue-winged Warbler, the result would have been a bird with the total genotype wwSsPP: in other words, a Blue-winged Warbler with intermediate wing-bars as described above.

Such a crossover can also readily account for other very rare combinations

which may appear. AMNH 506277, for example, is a typical male Golden-winged Warbler except that its wing-bars are of the intermediate type. Such a bird could be the offspring of a crossover Brewster's Warbler (like that described above) and a normal Golden-winged Warbler, and would have the genotype WWSspp.

Obviously only a small proportion of all Blue-winged or Golden-winged Warblers is of mixed ancestry, so the proportion of individuals with intermediate wing-bars in a series of either parent from all over the range of the species is small. On the other hand, *all* Lawrence's Warblers are obviously of mixed descent, so that a higher proportion of crossover types should be found in a series of these hybrids. My observations confirm this: of 17 Lawrence's Warblers examined, 13 had the normally expected Blue-winged Warbler type of wing-bar, and 4 were intermediate, indicating a crossover parent (or earlier ancestor).

Genetic Problems for Future Study

Although I believe the genetic theories outlined in this paper to be basically correct, some of them are admittedly oversimple. This is especially true of that concerning the inheritance of white versus yellow underparts. The *presence* or *absence* of yellow seems to follow the pattern of inheritance described quite closely. As yet, however, no hypothesis has been worked out to account for the great variation which exists in the *extent* of this yellow, both in Brewster's Warblers and in heterozygous Golden-winged Warblers (of which CNHM 148778 probably represents the extreme development). This is probably a matter of quantitative inheritance based on the interaction of several genes, the exact number of which will perhaps never be known.

Another variation of which the genetic basis is uncertain is that of the transocular black line. In occasional specimens of Brewster's Warbler (reference specimen UMMZ 73519) this normally thin line is expanded until it approaches the width of the black auricular patch normally present in the Golden-winged Warbler. Another case of linkage may be involved here, with one gene controlling the presence or absence of the throat-patch and the other the presence or absence of the transocular line enlargement. Brewster's and Blue-winged Warblers with expanded black transocular lines are so rare, however, that linkage must be particularly close, and crossovers consequently highly infrequent.

Correlation Between Genetic Theory and Field Work

There is great need for intensive field work in areas of heavy hybridization. Parent birds and their offspring should be color-banded and followed through successive seasons. Very few cases in which the parentage of a hybrid brood was unequivocally known and the brood followed through the post-juvenal

molt have been reported. The correlation between juvenal and later plumages is poorly known, and my own experience (Parkes, 1949) as well as that of Faxon (1911, 1913) and Nichols (in Carter, 1944) indicates that accurate prediction as to the type of plumage into which a given juvenal will molt is probably impossible.

The few cases of young birds of known parentage which have come to my attention all fit the basic genetic theories outlined in this paper. Faxon's 1911 paper summarized all such cases reported to that date, and his interpretations were essentially correct in the light of what was known at that time. He quoted one case (p. 69) reported by Beebe (1904) in which a male *lawrencei* was mated with a female *pinus*. All six of the offspring were described by Beebe as being typical *pinus*. Faxon could not understand why these young birds were identified as *pinus* rather than *lawrencei*. Beebe was correct, however, as according to the theories outlined here, the offspring of a mating between *lawrencei* and homozygous *pinus* should be phenotypically 100% *pinus*.

Summary

The Blue-winged Warbler (*Vermivora pinus*) and the Golden-winged Warbler (*V. chrysoptera*) hybridize over an extensive area of eastern North America where their respective ranges overlap, producing two general hybrid types. The commoner, Brewster's Warbler, is considered to be the F_1 offspring of the original interspecific cross. The rarer, Lawrence's Warbler, is considered to represent the combination of recessive characters. Two records are cited of supposed matings between Brewster's Warblers, but evidence is presented to indicate that back-crosses to a parental phenotype are the rule, and hybrid-hybrid crosses a rare exception, even when opportunity for such matings is present. The modes of inheritance for the throat and underparts colors are presented. The rare Lawrence's Warbler (recessive) type may be recovered by a number of possible crosses other than inter-hybrid matings.

Brewster's Warblers with yellowish underparts are considered to be mostly F_1 hybrids (plus the offspring of certain later crosses), while those with white underparts are back-crosses to the Golden-winged parent species. The allele for white underparts is considered incompletely dominant over that for yellow underparts. Heterozygous Golden-winged Warblers may be detected by this means. Chromosomal linkage is postulated for the genes determining underparts color and wing-bar type. Occasional variants from the expected character combinations are ascribed to a simple crossover. Other problems in the genetics of these birds are indicated, and the importance of field work in their study is emphasized.

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